Front. For. China (2006) 2: 176–181
DOI 10.1007/s 11461-006-0021-9

RESEARCH ARTICLE

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Physio-ecological response of *Haloxylon persicum* photosynthetic shoots to drought stress

Abstract This paper studied the seasonal characteristics to resist the drought stress of *Haloxylon persicum* Bge. Ex Boiss. et Buhse photosynthetic shoots at habitat. The results showed that the predominant drought resistance factors were varied at the different stage from growth to development. In the blooming season (from May 31 to June 29), endogenous ABA contents were rare; stomatal conductance and photosynthesis intensity were the highest at the whole stage from growth to development; soluble sugars contents had a decreasing trend and proline contents increased a little that made proline become the predominant factor to resist the drought under this light water stress. In the hot summer (from June 29 to July 26), ABA contents accumulated rapidly; stomatal conductance dropped to the lowest level of the growth and development; chlorophyll was also decomposed; both soluble sugars and proline contents showed the trend of quickly accumulating, but the former was faster than the latter. It was due to stomatal limitation and osmotic organic molecules accumulation that would affect the photosynthetic shoots to resist severe drought stress. At the late period of the development (from Aug 9 to Aug 22), ABA rapidly accumulated, its contents got to the highest level of whole life-span; stomatal conductance increased a little; proline and soluble sugars contents changed little at high level; while the ratios of ABA to CTK content and ABA to IAA content got up obviously, the effect to resist drought stress on high content ABA was inhibited by endogenous plant hormone CTK and IAA, then the continuing accumulation of proline and soluble sugars would be prevented. Osmosis of organic molecules was the most important factor to adjust leaves to severe water stress at this period.

Keywords *Haloxylon persicum*, drought stress, endogenous hormone, stomatal conductance, osmotic organic substance

1 Introduction

Haloxylon persicum is one of typical desert plants, which is mainly distributed on shifting or half-shifting sand dunes of narrow sub-desert areas in middle and west Asia. The species is also called super xerophyte due to its special drought tolerance that enables it to survive in prohibitive environments. Therefore, this species has been particularly selected as a pioneer plant to stabilize sand dunes, as well as an excellent plant material to investigate the physiological characteristics of stress adaptation (Zhang, 2002).

During drought stress, plant cells accumulate solutes such as proline rapidly to prevent water loss and to reestablish cell turgor, which is maintained by osmotic adjustment (OA) and this can improve drought-tolerance. It proved to be most effective among all stress adaptation mechanisms (Cushman, 2001). Soluble sugars (Munns and Weir, 1981; Johnson et al., 1984; Kameli and Lösel, 1995; Rekika et al., 1998) and proline (Tan and Halloran, 1982; Ali et al., 1994; Mattioni et al., 1997) level increased under water stress and are potentially important contributors to OA. Plant growth and response to a stress condition is largely under the control of the plant hormone ABA. The first response of all the plants to acute water deficit is the closure of their stomata to prevent the transpiration water loss. ABA promotes the efflux of ions from the guard cell, which resulted in the loss of turgor pressure leading to

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Translated from *Scientia Silvae Sinicae*, 2005, 41(5) [译自：林业科学, 2005, 41(5)]

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stomata closure (Leckie et al., 1998; Rock and Ng, 1999). Jackson et al. (1995) have reported that exponential relationships exist between stomatal conductance and ABA concentration in the xylem. Heckenberger et al. (1996) have reported that logarithmic relationships exist between stomatal conductance and exogenous ABA concentration when exogenously applied on the leaf. The soil desiccation resulted in the reduction in stomatal conductance and leaf growth even before there was any significant reduction in leaf cell turgor pressure (Gowing et al., 1992; Cramer, 1994; Dodd and Davies, 1996; Puliga et al., 1996). Under-water deficit conditions, auxin (indole-3-acetic acid, IAA), and ABA concentration in *Gossypium hirsutum* leaf increased and led to proline accumulation (Yuan and Ding, 1990). ABA/CTK (cytokinin) ratio changes to modulate the stomatal aperture (Ma and Liu, 1993) have often been reported. Various quantity ABA and CTK were externally added on *Avena* spp. seedlings and proline would be accumulated only when ABA/CTK ratio was greater than one; otherwise, the process of proline accumulation would not occur (Nie and Ma, 1994).

Under the natural water deficit conditions, the seasonal variations of concentrations of endogenous plant hormones, soluble sugars, free proline, chlorophyll and stomatal conductance were investigated in *H. persicum* photosynthetic shoots. The aim of the present work is to study the physiological responses and adaptations of *H. persicum* to drought stress and elucidate physiological adaptive mechanism survived in the hyper-arid desert.

2 Materials and methods

2.1 Description of study area

The study sites are located at the south-middle edge of the desert in Qitai County (44°18′N, 89°54′E), Xinjiang Uygur Autonomous Region, northwestern region of China. Annual precipitation and evaporative volume are 150–167 mm and 2,141 mm respectively. Annual radiation time is 2,840–3,230 h. The forest-free period is 156 days, temperature extremes can reach 41°C in summer.

2.2 Plant source

The first sampling was conducted on May 2, 2004, and after that, sampling was conducted every two weeks until September 5, 2005. The species studied was *H. persicum.* Three populations were chosen, and ten to fifteen mature plants per population were taken for the experiment. All plants selected were 2–3 m tall, about 10–15 years old, healthy and without infection. Care was taken to select the plants close to each other in each transect. Southward-facing plants (receiving maximum light during the day) were used for measurements.

2.3 Measurements

2.3.1 Stomatal conductance

Leaf conductance was determined on the fully expanded photosynthetic shoots using a steady state water-vapor diffusion parameter (Model LI-1600, LICOR Inc., Nebraska, USA). The average values on day 14 were calculated when seven conductance measurements were made at local time 8:00, 10:00, 12:00, 14:00, 16:00, 18:00 and 20:00, respectively.

2.3.2 Extraction and quantification of plant hormones using HPLC

Leaves (5 g) were ground with liquid nitrogen. Plant hormones were extracted in 30 mL of methanol at 4°C while being shaken overnight. Samples were centrifuged and the supernatant was collected and vacuum dried and subsequently dissolved in 100 μL of 10% CH_3CN. The plant hormones content was determined using HPLC analysis. An LC-10A TVP photodiode and ray detector (PDA), and a Shim pack CLC-C_8 (0.15 m×6.0ϕ) were used. The flow rate was 1.5 mL/min. Detection was at 250 nm at 30°C. The solvent for the pump A was 10% CH_3CN after the pH value was adjusted to 3.0 with CF_3COOH. The solvent for pump B was 60% CH_3CN. The ABA, IAA, gibberellic acid (GA_3), and CTK standard were purchased from Aldrich. The peak was identified and quantified against the external standard. The retention time of standard peaks GA_3, IAA, CTK, and ABA were 6.338, 9.965, 11.189, and 17.763 min, respectively.

2.3.3 Proline extraction

The proline content was estimated using the method of Zhou (1995). The plant material was homogenized in 3% aqueous sulfosalicylic acid, and the homogenate was centrifuged for 10 min at 8,000×*g*. The supernatant was used for estimating the proline content. The reaction mixture consisted of 0.2 mL of supernatant, 2 mL of acid ninhydrin, and 2 mL of glacial acetic acid, which was boiled at 100°C for 1 h. After termination of the reaction in an ice bath, the reaction mixture was extracted with 4 mL of toluene. The absorbance was at 520 nm.

2.3.4 Analysis of soluble sugars

Freeze-dried leaves (50 mg) were ground and extracted in 1 mL of 80% (v/v) ethanol. For recovery purposes, a known amount of ribitol was added to the extracts as an internal standard. The extracts were then boiled for 15 min and centrifuged for 5 min at 10,000×*g*. The supernatant was removed and the pellet was extracted twice as above. The extracts were vacuum dried at 45°C. The dried extracts were re-dissolved in 1 mL of distilled water and purified using anion exchange (Sephadex QAE-A-25, Pharmacia Biotech, Sweden). The eluates (1 mL of extract and 2 mL of water washings) were vacuum dried and re-dissolved in 300 µL of water. Hexose (glucose and fructose) and sucrose were analyzed at 35°C using an HPLC equipped with a 300 mm×7.8 mm column (carbohydrate-H^+, HYDERSIL, UK). H_2SO_4 (0.005 mol/L) was used as the solvent at a flow rate of 0.6 mL/min.

2.3.5 Analysis of chlorophyll

Shoot samples were extracted overnight at 4°C in 80% (v/v) aqueous acetone and chlorophyll content was measured by UV-265 spectrophotometer.

2.3.6 Photosynthetic shoots water status

The photosynthetic shoots were weighed (FW) and the dry weight (DW) was measured after drying at 80°C for 24 h. Relative water content (*RWC*) was calculated using the formula: *RWC* = [(FW-DW)/FW] ×100%

2.3.7 Soil water status

The volumetric soil water content was measured in each soil column within the 0–100 cm layer, and three random samples were taken every 10 cm, and after oven drying at 80°C for 48 h, soil water content was calculated.

3 Results

3.1 Photosynthetic shoots response to seasonal change of drought stress

H. persicum bloomeds in the later part of May until early June, and florescence lasted for half a month. It was shown in Fig. 1 and Table 1 that during the blooming season, soil water content was 2.87 and 3.12 g/kg on May 31 and June 14, respectively. Water content in photosynthetic shoots reached the highest level of the whole growth season, 65.2 and 57.4 g/kg, respectively. Stomatal conductance was also the highest level of the whole growth season 0.48 and 0.46 mol/(m^2·s), respectively. Photosynthetic shoots were lightly subjected to water deficit. After the blooming season and followed by a hot summer, *H. persicum* entered the period of reproductive development dormancy. Soil water content was 1.16 g/kg, water content in photosynthetic shoots was reduced to 49.7 g/kg and stomatal conductance was also rapidly reduced to 0.3 mol/(m^2·s). Stomotal conductance was continuously reduced to 0.23 and 0.25 mol/(m^2·s) on July 12 and July 26, respectively. At the same time, soil water content was 1.07 and 0.98 g/kg, respectively, and wilting of photosynthetic shoots occurred due to the heavy drought stress. The transpiration water loss decreased since August, and water content in photosynthetic shoots was about 50 g/kg. Soil water content was 1.56 and 1.87 g/kg on Aug 9 and Aug 22, respectively. Stomatal conductance increased to 0.31 and 0.33 mol/(m^2·s), respectively, and these changes led to the expansion of photosynthetic shoots and there was a significant reduction on the wilting degree of photosynthetic shoots.

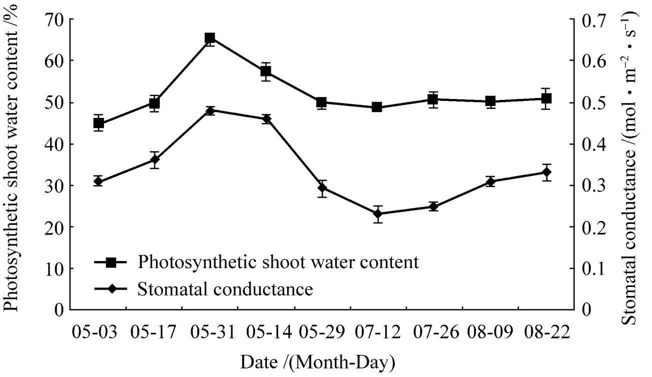

Fig. 1 Seasonal changes of LWC and stomatal conductance in *H. persicum* photosynthetic shoot

Table 1 Seasonal changes of soil water content

Date (Month-Day)	05-03	05-17	05-31	06-14	06-29	07-12	07-26	08-09	08-22
Soil water content /(g·kg^{-1})	1.76±0.12	1.85±0.15	2.87±0.18	3.12±0.20	1.16±0.11	1.07±0.09	0.98±0.09	1.56±0.08	1.87±0.09

Values are means ± s.d.

3.2 Proline and soluble sugars content response to seasonal change of drought stress

Seasonal changes of proline and soluble sugars content, which function as osmolytes in photosynthetic shoots, are shown in Fig. 2. During the blooming season from May 31 to June 29, soluble sugars content in photosynthetic shoots reached the lowest level (9.17 mg/g DW) in the whole growth seasons, whereas, chlorophyll content reached the highest level (91.2 mg/cm^2), and proline content slightly increased. Soluble sugars as well as proline accumulated rapidly during the period from June 29 to July 12, and their content, compared with the changes of June 29, increased to five and twofold on July 12, respectively, whereas the chlorophyll content rapidly decreased to a relatively low level of 70.4 mg/cm^2. Sugars and proline continued to accumulate to 5.5- and 2.7-fold on July 26 than the value of the content on June 29, respectively. Followed by relative high level of contents until Aug 22, chlorophyll contents were at a relatively low level.

Soluble sugars removed from photosynthetic shoots to blossom apparatus functioned in supplying nutrient substance for blooming in the blooming season, thereby reducing the soluble sugars content in photosynthetic shoots. At the same time, photosynthetic shoots were in a light drought stress due to maintenance of water contents in photosynthetic shoots ranging from 57.4 to 65.2 g/kg, and triggered proline contents a slight increase earlier than soluble sugars content. In the hot summer from June 29 to July 26, photosynthetic shoots were in a severe drought stress due to maintenance of water contents in photosynthetic shoots ranging from 48.7 to 50.6 g/kg, soluble sugars and proline accumulated rapidly. The solutes that accumulated during the osmotic adjustment helped in adaptation to drought stress. Followed by maintenance of relative high contents of soluble sugars and proline, there no manifest reduction occurred.

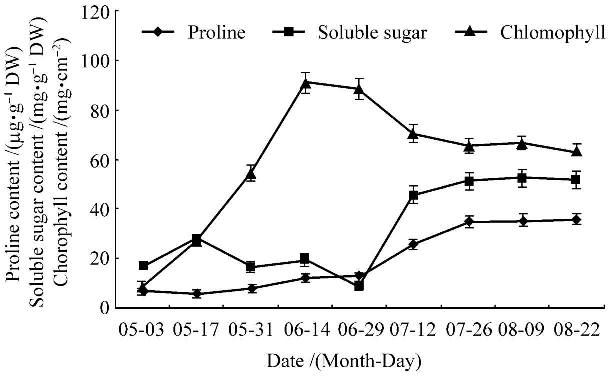

Fig. 2 Seasonal changes of chlorophyll, soluble sugars and proline content in *H. persicum* photosynthetic shoot Chlorophyll content (mg/cm^2), soluble sugars content (mg/g DW), proline content (μg/g DW)

3.3 Plant hormones response to seasonal change of drought stress

Four kinds of endogenous plant hormones in photosynthetic shoots showed seasonal variation (Fig. 3). In the early growth season from May 3 to May 31, GA_3, IAA, and CTK contents reached a relative high level to the whole growth season. In the blooming season from May 31 to June 29, GA_3, IAA, and CTK contents that occurred manifested reduction and maintained changes of the low level, whereas ABA contents increased slightly to be contributed to adjust and adapt an environment to cope the light drought stress. In the hot summer from June 29 to July 26, the changing trend that GA_3 and ABA contents increased quickly more than IAA and CTK contents obviously occurred. In the late growth season from July 26 to Aug 22, GA_3 presented an obviously decreasing trend, and IAA and CTK contents still maintained a relative high level in contrast to GA_3 contents, whereas, ABA contents increased rapidly due to be accumulated to cope and resist drought stress.

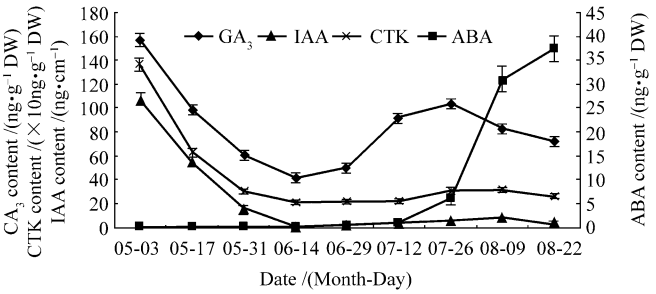

Fig. 3 Seasonal changes of four endogenous plant hormones content in *H. persicum* photosynthetic shoot

3.4 The relationship of C_{ABA}/C_{CTK}, C_{ABA}/C_{IAA} and proline accumulation

It is shown in Figs. 2, 3, and 4 that at the period of light drought stress from May 31 to June 29, there were traces of ABA 0.15 ng/g DW in photosynthetic shoots, and both C_{ABA}/C_{CTK} ratio (the content of ABA to the content of CTK) and C_{ABA}/C_{IAA} ratio (the content of ABA to the content of IAA) were extremely small. At the period of severe drought stress from June 29 to July 26, both C_{ABA}/C_{CTK} ratio and C_{ABA}/C_{IAA} ratio showed ascending trends; meanwhile, proline content was also rapidly accumulated to the highest level of the whole growth season. When C_{ABA}/C_{CTK} ratio was 0.5 (on July 12), proline content increased acutely. Until C_{ABA}/C_{CTK} ratio and C_{ABA}/C_{IAA} ratio reached 2 and 1 (on July 26), respectively, maximum accumulation of proline in the whole growth season occurred. In the late growth season from July 26 to Aug 22, although C_{ABA}/C_{CTK} ratio and C_{ABA}/C_{IAA} ratio reached 14 and 8 (on Aug 22), respectively, proline contents stably maintained to fluctuate at the highest level of the whole growth season, and no continuously ascending trend was visible.

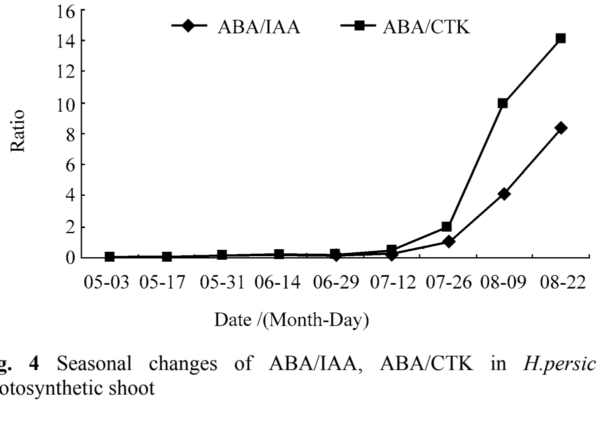

Fig. 4 Seasonal changes of ABA/IAA, ABA/CTK in *H.persicum* photosynthetic shoot

4 Discussions

Plants tend to cope with water deficit stress by synthesizing and accumulating some compatible solutes, which are termed as osmolytes. These compounds include proline, and soluble sugars are low molecular weight, highly soluble, and electrically neutral molecules, which are non-toxic even at molar concentrations (Tang, 1998). In addition, the rapid increase in soluble sugars in response to water stress can be attributed to the property that they do not intervene with the normal metabolic processes of the cells and decrease enzymatic activity, and slower consumption due to decreased growth and starch hydrolyze made it sufficient to be supplied (Liu, 1992).

Stomatal limitation was generally accepted to be the main determinant of reduced photosynthesis in perennial woody orchard species under light drought stress, whereas non-stomatal effects through increasing concentration of synthesized protein more than de-gradated protein. Decreasing concentration of chlorophyll due to increases in chloroplast degradation was attributed for the limitation of photosynthesis under moderate or severe drought conditions (Xia, 1993). It is shown in Figs. 1 and 2 that there was a significant increase in the concentration of chlorophyll as well as stomatal conductance in the blooming season (from May 31 to June 29), Mazongren (1993) reported that changes in stomatal opening would result in accumulation of proline, and a high degree of co-regulation exists between proline accumulation and reduced quantity of oxygen in plant. Stomatal closure due to drought stress would cause depression in oxygen uptake, which involved in inhibiting activities of proline oxidase, the reduced activity of proline oxidase, under water stress, has been suggested as a factor causing proline accumulation in stressed tissues.

In the hot summer from June 29 to July 26, stomatal conductance reduced to the minimum of the whole growth season showed that the stomatal opening was obviously depressed under a severe water stress. Stomatal limitation was contributed to acute accumulation in proline as well as a decrease in photosynthesis intensity, which resulted in a limitation in chloroplast metabolism, and this limitation was implicated due to degradation of chlorophyll as well as decreased synthesis of protein under drought, which finally inhibited total photosynthetic metabolism. These studies indicated that reduction of chlorophyll content could be used as an indicator to estimate that irreversible damage to organ should be taking place in photosynthetic shoots, or there was a metabolic impairment with increasing drought stress. In the latter part of the whole growth season from July 26 to Aug 22, the high concentration of proline and soluble sugars still remained constant via slightly increased stomatal conductance as well as adjustment by endogenous plant hormones.

It is shown in Figs. 1, 2, and 3 that in the blooming season from May 31 to June 29 *H. persicum* was subjected to a slight water stress, and there were traces of ABA in photosynthetic shoots, and stomatal conductance varied ranging from 0.292 to 0.481 mol/(m^2·s), and a decline trend in soluble sugars content and an ascending trend in proline content occurred. In the hot summer from June 29 to July 26, ABA was accumulated rapidly, and stomatal conductance varied ranging from 0.232 to 0.292 mol/(m^2·s). Under extremely drought conditions of hot summer, ABA in mesophyll cell was rapidly diverted to the cuticle of photosynthetic shoots to protect them from drought by inhibiting stomatal opening, as the process caused a decrease in transpiration water loss. Meanwhile, both soluble sugars and proline content presented acute accumulating trends, and accumulating intensity in the former was greater than in the latter. this indicated that soluble sugars and proline acted in coordination, thereby regulating plants to adapt to severe drought stress. In the latter part of the whole growth season from Aug 9 to Aug 22, ABA accumulation reached 36-fold than that on 12 July, whereas stomatal conductance increased slightly, and proline as well as soluble sugars contents also remained as a relative high level constant, and no continuously ascending trend was visible. It was suggested that at this stage, photosynthetic shoots were still subjected to severe drought stress; however, continuous process in proline and soluble sugars accumulation was inhibited, since stomatal conductance increased might due increased CTK and IAA concentration in photosynthetic shoots promote stomatal opening directly as well as decrease the sensitivity of stomata towards ABA, the physiological process in response to drought stress of high concentration ABA which was transported from the xylem sap in root to photosynthetic shoots was inhibited by CTK and IAA (see Fig. 4).

Various stress factors in photosynthetic shoots responded to drought in different ways, depending on progressive degree of drought. In the blooming season from May 31 to June 29, proline content slightly increased, which was attributed for light water stress conditions during this stage. In the hot summer from June 29 to July 26, accumulating intensity in soluble sugars was greater than in proline, and ABA was also accumulated rapidly. When $C_{\mathrm{ABA}}/C_{\mathrm{CTK}}$ ratio was 0.5 (on July 12), proline content increased acutely. Until $C_{\mathrm{ABA}}/C_{\mathrm{CTK}}$ ratio and $C_{\mathrm{ABA}}/C_{\mathrm{IAA}}$ ratio reached 2 and 1 (on July 26), respectively, maximum accumulation of proline in the whole growth season occurred.

Acknowledgements This study was financially supported by the National Natural Science Foundation of China (Grant No. 30470330 and 90502004).

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